

CARNIVOROUS PLANT NEWSLETTER

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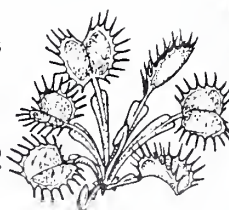




CARNIVOROUS PLANT NEWSLETTER

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Front Cover: *Drosera indica* red form with orange flowers. Photo by Phill Mann.
Rear Cover: A plant from the *Drosera petiolaris* complex. Photo by Phill Mann.

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Editorial

BARRY MEYERS-RICE

I looked with disbelief at my computer screen. The email from Rick Walker was jarring. Rick, president of the International Carnivorous Plant Society, had just informed me that Don Schnell was retiring from his editorial role at CPN. I read the message again. I blinked several times. The cursor on the screen blinked back, expectant.

Don Schnell leaving CPN after twenty-five years? Unacceptable! He was a fixture! When I was first learning about carnivorous plants, Don's book was frequently on my reading pile. Then as a CPN reader, Don's articles, photo essays, and reviews were my favorite features. And when I started writing contributions for CPN, Don always had suggestions on how to improve my work. But now this cofounder of CPN was retiring? And Rick wanted me to join the crew as a new co-editor? I was honored. Certainly, it was an offer I would not refuse. I emailed my acceptance to Rick.

The next time you get lost in your back issues of CPN, ponder the path the newsletter pioneered over the decades. After promising starts, many carnivorous plant journals have descended into the dregs of pure novelty interest, just to die as rapidly as they began. But under careful stewardship, CPN survived its adolescence and matured into a well respected resource. It provides a rich mulch of information for the cultivator, field reports for those who long for the smell of *Sphagnum* in the morning, and a prestigious home for scientific articles.

Reviewing the developments of just the last ten years testifies to how CPN has recorded exciting times. CPN followed the explosion of information and interest in South America—both on the tepuis and off. It taught us about the pygmy, tuberous, and tropical sundews of Australia. It documented the increased interest in *Utricularia* which followed the publication of Peter Taylor's monograph. And it tracked the increasing importance of tissue culture and the internet—two high-tech disciplines that may seem foreign to the traditional enthusiast who is often soiled from head to toe with peat and perlite.

At the same time, articles in CPN have noted that not all is well for our beloved plants. More than 95% of the wetland habitats in the U.S. have been drained or developed. Global habitat destruction is accelerating. Reports from those visiting *Nepenthes* habitats rarely contain good news. Some carnivorous plants are extinct, while many others are endangered. CPN has kept us updated on the alphabet soup of laws, treaties, and organizations (ESA, CITES, IUCN, USFW, WWF, etc.) as well as the unfortunate disdain and backlash that many of these regulations have engendered.

Although CPN is already a magazine of great quality, it must continue to grow and improve. Jan's and my duties are clear. We have been redesigning the editorial process to accommodate the international nature of CPN's staff and its contributors. We have been reworking the prepublication machinations so your articles will appear in print with an absolute minimum of errors. We have been exploring the technological solutions (and new problems) introduced by the internet. And we will be maintaining and encouraging the diversity of articles in the newsletter. While we are implementing these improvements, what will you do to

help CPN? Our mailboxes are waiting to hear from you—if you are still pondering whether you should write that article, turn on your word processor or typewriter and get to work!

I am writing this editorial on Christmas day, so if Don's departure has left me bogged in maudlin sentimentality I hope you understand. We hope the inevitable changes in CPN will be for the better. Jan is a consummate botanist and will be the primary editor for articles addressing taxonomical issues. I too am a scientist, and will be editing your articles on conservation, cultivation, and field trips. Together we will do our best to fill Don's waders. And while that editor emeritus is no longer at CPN's helm, his influence is indelible.

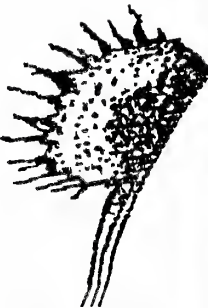
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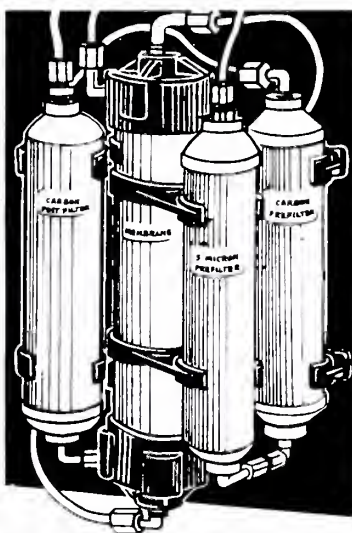
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“New” data relating to the evolution and phylogeny of some carnivorous plant families

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Date received: 31 March 1996

Keywords: evolution—physiology— taxonomy.

In recent times several papers appeared dealing with the systematic arrangement of several families of carnivorous plants by DNA sequence alignment and homology comparison (Albert *et al.*, 1992; Conran & Dowd, 1993; Cameron *et al.*, 1995). One rather surprising result of this work was an apparent affinity of Byblidaceae to several families of “sympetalous” dicotyledons. This could mean that *Byblis* is related to the order Scrophulariales which also contains the carnivorous family Lentibulariaceae and the sub-carnivorous genus *Ibicella* (*Martynia* p.p., Martyniaceae/Pedaliaceae p.p.).

Another even more striking result is the grouping of Droseraceae, Drosophyllaceae (the separation of *Drosophyllum* from Droseraceae is also supported by DNA analysis), Dioncophyllaceae, Ancistrocladaceae, Nepenthaceae, Plumbaginaceae, Polygonaceae, and Simmondsiaceae together in one clade to which the couple Tamaricaceae/Frankeniaceae is the closest sister clade (see Figure 1). This grouping is so striking because it unites families which have been assigned to numerous orders in previous systems (e.g. Saxifragales, Theales, Aristolochiales, Primulales, Caryophyllales, Euphorbiales), formerly believed to constitute widely distinct groups. But it is especially interesting because it now brings several carnivorous families into close proximity to each other. Additionally, a phytochemical characteristic, viz. the presence of the acetogenic naphthoquinone plumbagin in Droseraceae, Drosophyllaceae, Dioncophyllaceae, Ancistrocladaceae, Nepenthaceae, and Plumbaginaceae, and biosynthetically related anthraquinones in Polygonaceae (Hegnauer, 1989) lends further strong support to the assumption that this grouping is not an artificial one (plumbagin is only found in very few other families of flowering plants like Ebenaceae—which group close to Ericales according to DNA data and thus do not seem to belong to the “carnivorous” plumbagin clade—and several monocotyledons—which are certainly not closely related to this group). The genetical methods cannot yet resolve the exact relationships within the new clade defined (cf. the unresolved trichotomies in the diagram, this will certainly improve as soon as additional data become available), and character distributions within this clade are somewhat reticulate.

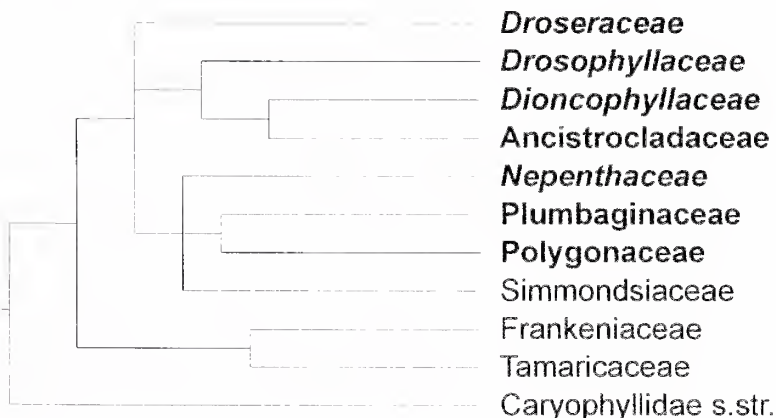
Instantly, the question arose if morphological characteristics could be found in the new cousins of the carnivores which indicated a sub-carnivorous condition in these (i.e. predispositions to the carnivorous habits presumably evolved later on). An examination of Ancistrocladaceae (consisting only of the small palaeotropical genus *Ancistrocladus* which is known for some time to be the closest relative of Dioncophyllaceae, sharing e.g. similar pollen and petiole structure and the unique naphthyl-isoquinoline alkaloids, cf. Bringmann & Pokorny, 1995) yielded no compelling results. But even the closest relatives of *Triphyphyllum* (viz. the other two members of Dioncophyllaceae, *Habropetalum* and *Dioncophyllum*, which are non-carnivorous) do not show any obvious sign of the striking features observable

in the trapping leaves of *Triphyophyllum*. Nevertheless, there are some apparently bridging features to Nepenthaceae (which overlap in some parts of the distributional range with Ancistrocladaceae), viz. a rather unusual anatomy of the petiole base (Metcalf, 1951).

The more striking it is when we direct our attention to another, superficially rather inconspicuous family, viz. Plumbaginaceae. This family is characterized by the possession of specialized glands secreting lime and/or mucilage (licopolitan or mettenian glands). These glands were studied in some detail more than hundred years ago (Wilson, 1890). Already then a close resemblance of these to the salt glands found in Frankeniaceae and Tamaricaceae was noted. The recent genetical studies mentioned showed that phylogenetic relations between these families seem likely. Additionally, glands resembling to some degree the sessile ones of Plumbaginaceae can be observed on the leaf surfaces of *Ancistrocladus* and *Nepenthes*.

More recent research (Rachmilevitz & Joel, 1976; Fahn, 1979) revealed anatomical details of the specialized mucilage calyx glands of *Plumbago*. These glands show some peculiar features which are found to recur in the tentacles of *Drosera*, *Drosophyllum* and *Triphyophyllum*. They are borne on multicellular stalks with an epidermis and several layers of underlying parenchyma, thus constituting emergences. The glandular portion consisting of several layers of secretory cells is separated from the parenchyma of the supporting stalk by a single or few layers of cutinized cells forming an endodermis exactly like in the tentacles of the mentioned carnivores. Additionally—and this is almost unique in this group—a vascular strand sometimes enters the parenchymatous core of the stalk for some distance. Therefore, the calyx glands of Plumbago display features which render

Phylogenetic reconstruction by rbcL sequence comparison
augmented by phytochemical and anatomical data



bold: families containing acetogenic quinones
italic: families containing carnivorous genera

Figure 1

them “almost complete” precursors or evolutionary prototypes of the tentacles of the mentioned adhesive carnivorous plants. Some species of *Plumbago* (e.g. *P. tristis*) and many representatives of *Ceratostigma* and *Dyerophytum* have either glabrous calyces or emergences on the calyx which do not bear a glandular head. *Plumbagella*, a seemingly more advanced (annual, temperate) descendant of *Plumbago* (perennial, subtropical to tropical) does share the glandular emergences with this genus. It has been argued that the bristles and sticky secretions of the calyx of these genera (which together form the subfamily Plumbaginoideae—the other subfamily, viz. Staticoideae apparently lacks plumbagin) aid in seed dispersal by animals, ensuring an attachment to the coat or plumage of these (Fahn & Werker, 1972). The single-seeded fruits of these plants remain in the calyx and are easily detached together with it from the fruiting pedicels. Subsequent observations (Rivadavia, 1996) on *P. auriculata* showed that small ants were found trapped on the sticky glands of the calyx of this species. Thus, it can be assumed that an additional function in at least the glandular species is the exclusion of crawling insects from the flowers, thereby favouring flying pollinators which more effectively assure cross pollination (crawlers tend to visit all the flowers of the inflorescence of a single individual while flying insects more frequently change between several different inflorescences and individuals). The following hypothetical course of events can be formulated:

1. An evolution of the floral biology affecting first seed dispersal (from glabrous to bristly calyx) led to the formation of bristly emergences on the outer (abaxial) sepal epidermis. Recent representatives of the “primitive” stage are found in *Dyerophytum*, the more “advanced” condition is frequent in *Ceratostigma* and few species of *Plumbago*.

2. A further evolution of floral biology now affecting pollination (from bristly calyx to glandular calyx) led to glandular emergences, the vascularization of which could have rendered the process of secretion more effective. The glandular portion of these emergences was probably derived from the sessile glands of the leaf surfaces (suggested by structural similarities between both). Recent representatives of the “advanced” condition being many species of *Plumbago* and the single species of *Plumbagella*.

3. The crawlers frequently caught by the glandular emergences (which later became tentacles) were in some way utilized for the nutritional purposes of the plants—the adhesive trap was thus formed. Once this trapping strategy was successful, the other carnivorous features (like the irritability of the glands and the secretion of digestive enzymes) could have appeared by chance and were conserved by selection because they rendered ad hoc advantages over the individuals which did not display them.

4. The translocation of the tentacles to foliar surfaces (N.B. *Plumbago europaea* has vascularized bristles and *Plumbagella micrantha* has even stalked glands on the leaf margins, *Drosophyllum* has the tentacles on the abaxial surface of the leaves corresponding to the situation in the *Plumbago* calyx) rendered the traps more efficient in *Drosophyllum* and *Triphyophyllum*.

5. The integration of perceptive, motile, and digestive functions in the tentacles as well as a translocation to the upper, adaxial surface of the leaves constituted further refinements of the traps in Droseraceae (*Drosera*).

6. At some stage of this development, the springtrap mechanisms of *Aldrovanda* and *Dionaea* diverged from possibly adhesive precursors (but not necessarily from *Drosera*).

Fortunately, recent examples of these stages are extant (many of which found in the single subfamily Plumbaginoidae). Of course it must be borne in mind that the respective representatives are descendants of evolutionary intermediates and not the intermediates themselves.

Now it may be asked how Nepenthaceae could be integrated into the "emergent" scenery. But there may even be an answer to this one presented by Plumbaginaceae. Wilson (1890:244) writes, discussing *Aegialitis annulata*: "The petiole is of considerable length, and amplexicaul to a great degree. The inspection of a piece of epidermis from its base at once reminds one of the 'digestive surface' of *Nepenthes*", and when he continues "The similarity is only superficial, for in *Nepenthes* the glands lie at the termination of vascular traces, whereas the mucilage-glands of *Aegialitis* and all other Plumbagineae have no such connection," he thereby possibly even emphasizes this similarity because the same degree of parallelism can be observed between *Plumbago*/*Plumbagella* (where the glands are sometimes approached but in most cases not reached by vascular traces) and the adhesive carnivorous plants (in which the glands lie at the termination of the vessels). About *Plumbago scandens*, Wilson (1890:247) writes: "Spiral vessels pass up a greater or less distance into the stalks. Seeing, however that vessels are found penetrating simple emergences e.g. in *Ceratostigma*, etc., no special significance attaches to them in connection with the glands" but in the light of the notes made above, it seems that very special significance attaches to them in connection with carnivorous plant evolution!

It might be added that *Aegialitis* is considered a relict in the mangroves of the tropics of southeast Asia and north Australia, not closely related to any of the remaining members of Plumbaginaceae (which are predominantly more temperate). The glands on the surface of the leaves probably serve the purpose of secreting the excess of salt taken up with the brackish water the plants grow in. The similarity to *Nepenthes* is certainly not very far reaching and the pitchers of this genus remain unique organs in the plant kingdom.

It is interesting to see that most of the data mentioned here were known and published more than hundred years ago and only fifteen years after carnivory in plants was appreciated scientifically (Darwin, 1875). Nevertheless, only genetic and phytochemical results forced our awareness towards the conspicuous morphological parallels between Plumbaginaceae and several carnivorous plants.

Acknowledgements

I wish to thank the Director and staff at the Botanical Garden of Würzburg who supplied flowering material of *Plumbago indica*. Special thanks are due to Mr. Fernando Rivadavia from Sao Paulo, Brazil, who made important field observations on *Plumbago auriculata* mentioned above, and who sent liquid preserved material of this species.

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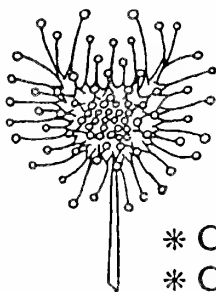
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Carnivory of *Byblis* revisited—A simple method for enzyme testing on carnivorous plants

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Keywords: carnivory: *Byblis*—carnivory: *Drosera*—carnivory: *Roridula dentata*.

Introduction and theory

At the beginning of this year I had a conversation with Dr. Jan Schlauer from the University of Würzburg (Germany) concerning carnivorous plants (CPs). In the course of this he mentioned a report by Heslop-Harrison and Knox (1971) in which the authors described an easy method to detect enzyme activities in carnivorous plants using photographic film. This seemed so interesting to me that I decided immediately to try this out. The following day I spoke to an acquaintance in Switzerland (Luigi Francini), whose hobby is photography and who has a small photographic laboratory. I asked if he would be willing to develop some film for me. Luigi Francini (who also has some CP at home) was enthusiastic, and after a quick lesson about different materials used for photography the first tests started the following weekend.

The theory is quite simple. Digestive enzymes dissolve the gelatine layer of exposed film. The gel contains the finely distributed photosensitive chemicals such as halogenous silver crystals, pigments, etc., and is applied as an extremely thin suspension onto the plastic substrate which is mostly made from acetylcellulose or polycarbonate. Strips of processed but not fixed Kodalith ortho (ASA 12) black and white film are used for the test.

The enzyme production of the plants is triggered by a yeast solution. Twelve hours later some dexterity is required to fix the film strips onto the trapping leaves. After removal twenty-four hours later, the strips show a typical spotting if enzymes are present. Laboratory examination of enzymes (e.g. with protein gels) is very expensive whereas this procedure with customary films is a very simple alternative, is very low-priced (only 1 or 2 cents per test!), and is thus really interesting for use in private greenhouses and even for field tests if accordingly adapted.

Suitable photographic material and its application

As mentioned above, Kodalith ortho (black and white) film is used in the literature, mainly for lithography, microphotography, and other industrial purposes because it is very robust and provides a wide range of contrast. It is an industrial film which usually must be specially ordered by photo shops. Since it was not easily available, I decided to test some different types of customary material with varying gelatine layers.

Luigi Francini recommended three different types of ILFORD black and white films. The more photosensitive this film is, the thicker it is and the more coarse

grained its halogenous silver crystals are. A series of tests were used to show which material was most suitable. ILFORD FP4 (ASA 125), ILFORD HP5 (ASA 400) and ILFORD XP2 (ASA 400) were tested on *Drosera capensis*, *Drosera cuneifolia* and *Byblis liniflora*. Instead of the method described in literature, I used only exposed (and not additionally processed and unfixed) material because it was my idea to find a test which was practicable and easy as possible. To stabilise the results on the strips after the exposure to the plants for further photographs, they were processed but not fixed by Luigi Francini and afterwards showed finer and durable details.

Significantly clearer results could be seen on the two coarse grained ASA 400 negatives (which had the thicker gelatine layer). Some looked like 'X-ray' images so the test plant could often be identified, whereas the FP4 ASA 125 was much lower in quality (where in one case a *Drosera cuneifolia* fed with a mosquito larva digested a 2 mm hole into the gel). Even after processing, the negatives of the sundews showed only a few, poor spottings and *Byblis liniflora* showed nothing. This result was surprising to me, because the Kodalith ortho film used in literature has only a sensitivity of ASA 12.

The negatives of the HP5 and XP2 showed the enzyme activities exactly the other way around, meaning black and white in reverse. Held against the light, the XP2 showed the clearest outlines of glue drops and (in excellent cases) even of the tentacles, so that it displayed nearly a complete image of the trapping leaf. The colour of the whole leaf area is light to pale grey, perhaps caused both by soaking the gelatine or by leaching soluble parts of the layer by humidity during the exposure to the plant. It was not a result of enzyme activity because the same effect also took place with pure water. More interesting were the black centres with clear perforations. Here the gel was dissolved by enzyme. The light shining through those holes in the layer and the black zones around provide a good contrast. For this reason the ILFORD XP2 was chosen as the most suitable film.

To expose the film I pulled it out of the roll and cut it into 1.0 to 2.5 cm wide strips, according to the size of the plant to be examined. To mark the film type and assigned plant durably (and in a way that would not be obliterated by the processing-bath) I cut different notches into the strips. Dates were conscientiously recorded. As mentioned above, correct fastening of the film strips on the trapping leaves of CPs needs a little imagination to achieve good "illustrations!"

Choice of suitable CPs

To check the methods, I chose adult plants of *Drosera capensis* and *Drosera cuneifolia* as references, because the enzyme production of sundews (*Drosera*) has been thoroughly examined and proven. In addition I used a one-year old rainbow plant (*Byblis liniflora*) of which the production of enzymes was still unclear. Bruce (1905) did some investigations on *Byblis gigantea* growing near Perth in Western Australia that showed positive results, but did not examine *Byblis liniflora*.

This question of carnivory for *Byblis liniflora* was of special interest to me since I had visited some north Australian habitats with my wife Irmgard, and we demonstrated a mutualism involving Capsid bug species (Miridae) and *Byblis liniflora* on our video (Hartmeyer & Hartmeyer 1995). That symbiosis showed much similarity with the two species of the South African *Roridula* and their *Pameridea*-bugs, which are also true bugs belonging to the Miridae. We observed this symbiosis for six years in our living-room in Weil am Rhein, and got some nice video shots which can be seen on our video (Hartmeyer & Hartmeyer 1994). However, a number of experts do not include *Roridula* with CPs because it shows no enzyme production. If the tests proved that *Byblis* does not produce enzymes and also shows the same sym-

biosis with closely related Capsid bugs, a new discussion by the experts about the assignment of the Rainbow Plant as a CP would be necessary.

This line of thought is particularly interesting because of the current discussion about the plumbagin branch of CPs. Plumbagin is a compound present in the "old" CP families Droseraceae, Drosophyllaceae, Nepenthaceae and Dioncophyllaceae, in which all species are able to produce proteolytic enzymes (Schlauer 1997). Observing the 'plumbagin-free' branches, only the two "modern" CP families Cephalotaceae and Lentibulariaceae show this uniform behaviour. All other families have at least members which do not produce enzymes. Even the Sarraceniaceae, which are the stars of nearly every CP book, contains such plants, e.g. *Darlingtonia* and several species of *Heliophora*. Interestingly, without any own enzymes those plants make numerous bacteria and arthropods do the digesting. This was confirmed recently by Ellis & Midgley (1996), who did large-scale tests with isotope-labelled (^{15}N) flies on *Roridula* associated with *Pameridea* bug populations. They observed that the isotopes sucked out of the prepared insects by the resident Capsid bugs reached the plant leaves via the feces dropped on the leaves, and were being absorbed probably through stomata. So it has been proven that *Roridula* is able to benefit directly from the wide selection of prey sticking to its leaves and not only via soil fertilisation by the natural decay of its prey.

The results of further enzyme tests can contribute to the clarification of the questions of carnivory—whether in the future some of those plants assigned today as true CPs (e.g. *Byblis*, *Darlingtonia*, *Heliophora*) may not be classified carnivorous anymore, or if the definition for a true CP must be reformed to allow for enzyme-free, and passive predigestion by symbiotes.

Enzyme production

In the literature, a yeast solution is used to trigger the enzyme production by the plants. Some tests with pure yeast, as well as solutions diluted by water, all showed a clear reaction from *Drosera*, which meant the tentacles and sometimes the whole leaf started to surround the treated spot.

If the solution was too concentrated coarse lumps appeared on the traps. This resulted in low quality illustrations of the tentacles and glue drop contours on the film. Pure yeast and dried mosquito larvae (which showed the strongest reaction!) yielded similar results.

The best results were achieved by a 10% solution of yeast in water. Depending on the trap size, one to three drops were applied using a small pipette. This procedure resulted in the most detailed outlines and was digested by all the plants without problems.

Preparing the series of tests

The tests described above yielded a second result concerning *Byblis* that I did not expect to be so unequivocal. On ASA 400 material all *Drosera* appeared as clear positive, but no *Byblis* showed enzyme production. To explore this result (which is surprising for what is usually considered a true CP), and to further test the whole laboratory procedure, I decided to follow the first tests with the following experiments:

- a) Nine different *Drosera* species as additional positive references. See Table 1
- b) Two specimens of *Roridula dentata* were tested three times, as negative references.
- c) Two specimens of *Byblis liniflora* were tested four times to confirm the results.

- d) *Drosera capensis aliciae* was tested twice to get a double-determination for this hybrid.
- e) *Drosera macrophylla* was fed with 1.5 mosquito larvae to check the strong enzyme reaction.
- f) The exposure time on the plants were increased from 24 to 32 hours to improve the quality of the images.

Results

The results of the new battery of experiments are as follows.

- a) All nine *Drosera* species showed unequivocal positive results.
- b) Ellis and Midgley (1996) used the Kodalith ortho film method by Heslop-Harrison and Knox (1971) for their investigations at the University of Cape Town. The negative results on *Roridula* were confirmed. More surprising were the holes in the gelatine layer caused by the *Roridula* leaf glands. On closer examination it became clear that the highly adhesive caoutchouc in the glue was damaging the gelatine layer. Every drop tore off parts of the gelatine when the strip was removed. So no enzyme activity was detected on *Roridula*. Under high magnification, the margins of the holes were clearly different from holes caused by proteolytic reaction.
- c) All tests on *Byblis liniflora* were negative.
- d) The two tests on *Drosera capensis aliciae* proved the reproducibility of the method.
- e) Again the dried mosquito larvae triggered the strongest enzyme production.

The chosen ILFORD XP2 material worked as expected and the increased exposure time also increased the illustration quality notably. The results were detailed images with a charming X-ray appeal even *without using processed and unfixed film*. But if processed, finer details of the images appeared, the durability of the negatives improved, and magnifications could be made. For documentation the strips were photographed on colour slide film, because the different grey-shades are reproduced much better than on black and white film, as Luigi Francini found out.

Conclusions

Using species of *Drosera* as a reference is recommended. The results of the tests on *Byblis liniflora* are a real surprise. Further experiments on other CP species are in preparation, but to describe them would go beyond the scope of this article. The described tests are not only very inexpensive (one film roll allows approximately fifty tests!), they are very easy to perform, show good reproducibility and are absolutely harmless for the examined plants. In fact, the more yeast or mosquito larvae are given to the plants, the more they benefit. These attributes make the test highly interesting for private CP collectors, and so (I hope) promise a flood of new test results if published for a wider, CP-interested, public. Easy field experiments are possible if the tested plants are sheltered against the weather during the exposition time.

A highlight of this study is the following: If a sensitive (e.g. ASA 400) conventional black and white film is used in the above described way, a reproducible and detailed low cost test without any chemical bath is possible!

Last but not least I would like to express my gratitude to Luigi Francini for his friendly support and professional treatment of all photographic works. And I wish success for everybody who tries the test, because I'm sure we can await further surprises on this subject.

Table 1: Test Results

Plant ^a	Appearance of the processed negatives	Enzyme activity ^b
<i>B. liniflora</i> ^c (15-19 cm tall)	Faint light outlines of the glue-drops were visible. No dark centres or perforation appeared.	—
<i>D. adela</i> (15 cm)	Clear light outlines contrasted with dark centres. The gelatine layer was partially perforated.	++
<i>D. aliciae</i> (4.5 cm)	Clear light outlines contrasted with dark centres. The gelatine layer had no perforations.	+
<i>D. browniana</i> (6 cm)	Clear light outlines contrasted with dark centres. Big (1-2 mm) holes occurred in the gelatine layer.	+++
<i>D. capensis</i> (14 cm)	Clear outlines contrasted with dark centres. The gelatine layer was partially perforated.	++
<i>D. capensis</i> × <i>aliciae</i> ^d (10 cm)	Clear light outlines contrasted with dark centres. The gelatine layer was strongly perforated.	+++
<i>D. capensis</i> × <i>aliciae</i> ^e (10 cm)	Clear light outlines contrasted with dark centres. The gelatine layer was strongly perforated.	+++
<i>D. cuneifolia</i> (6 cm)	Clear light outlines contrasted with dark centres. The gelatine layer was partially perforated.	++
<i>D. macrophylla</i> ^f (9 cm)	Clear light outlines contrasted with dark centres. Big (up to 10 mm!) holes inside the gelatine layer.	+++
<i>D. prolifera</i> (9 cm)	Clear outlines contrasted with dark centres. Gelatine layer was strongly perforated.	+++
<i>D. stolonifera</i> (15 cm, 11 cm tall)	Clear outlines contrasted with dark centres. The gelatine layer was partially perforated.	++
<i>R. dentata</i> ^g (18 cm, 28 cm tall)	No light contours or dark centres. Many small dot-like holes were visible inside the gelatine layer ^h .	—

Table 1: Results of the enzyme experiments performed 17 January 1997—26 January 1997.

(a) Measurements are for the plant's diameter, unless otherwise noted.

(b) Symbols used:

— Enzyme test negative

+ Enzyme test positive (Gelatine layer shows dark centres without perforation).

++ Enzyme test positive (Gelatine partially perforated).

+++ Enzyme test positive (Gelatine layer strongly perforated, possibly big holes).

- (c) Four separate tests were made.
- (d) Test 1.
- (e) Test 2.
- (f) Also fed 1.5 mosquito larvae.
- (g) Three separate tests were made.
- (h) Caused by tearing of the emulsion and not by enzymes (see the Results section)

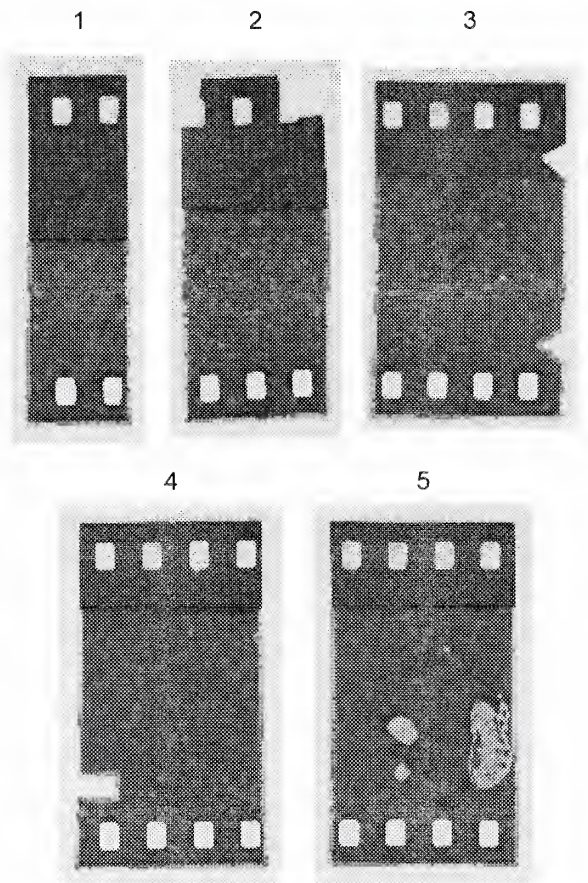


Figure 1: The film strips used to detect enzyme activity in various CP species.

Strip #	notches on the strips	species tested
1	none, narrow strip	<i>Byblis liniflora</i>
2	notch on perforation-side	<i>Roridula dentata</i>
3	two triangular notches	<i>Drosera capensis</i> × <i>aliciae</i> (Test 1)
4	one narrow notch	<i>Drosera adelae</i>
5	none, broad strip	<i>Drosera macrophylla</i>

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Nepenthes macfarlanei: Prey found in ground pitchers

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Keywords: carnivory: *Nepenthes macfarlanei*—carnivory: prey.

Nepenthes macfarlanei grows in the mossy montane forest of western Malaysia. Its ground and hanging pitchers are quite different in shape and colour. Ground pitchers with large, deep-red peristomes are often embedded in thick *Sphagnum* carpets (Figure 1). The upper part of the pitchers (peristome and lid) barely emerge from the moss layer.

In 1993 I had the opportunity to investigate some pitchers of *Nepenthes macfarlanei* on the mossy crest of Mount Brinchang (Cameron Highlands). In the following, I only mention animals found several times in the pitchers.

Hexapoda (insects)

Cockroaches (cf. *Ectobius*, Figure 2): These quick, mostly nocturnal insects are omnivorous. They like to make contact with their surroundings (which is called thigmotaxis). These animals climb without any difficulty over smooth surfaces with their pulvilli (small cushions on the legs with an adhesive function). It is astonishing that these animals are victims of *Nepenthes*! Their orientation is based on their antennae touching the environment incessantly. These antennae are the main source of tactile and chemical information. Therefore, it seems that cockroaches fall accidentally into the pitchers. But there is another question: Does the rotting material (digested animals with their smell) attract cockroaches (see also Cheek (1992))? Smaller beetles can also be found in pitchers, but in a lot of



Figure 1: Ground pitcher of *Nepenthes macfarlanei* embedded in *Sphagnum*.



Figure 2: Cockroach (cf. *Ectobius*)

ground pitchers, ants are by far the dominant prey (see discussion about ants by Erber (1979)).

Chilopoda (centipedes)

Scutigera (Figure 3) and *Scolopendra* (Figure 4, p50): Both of these centipedes have many legs and are extremely mobile, and are nocturnal. They are ground animals and predators which catch their prey by venomous claws. *Scutigera* also catches food with its long legs. It is one of the fastest centipedes. *Scutigera* has compound eyes, whereas *Scolopendra* is characterized by few ocelli. The activity of



Figure 3: Centipede (*Scutigera*)

these centipedes is correlated with hunger. Food (prey) is perceived by tactile and chemical receptors on mouth parts, legs, and antennae.

Arachnida (spiders and mites)

Spiders (Figure 5, p50) have in most cases several eyes, chemoreceptors, and systems highly sensitive to tactile stimulation and vibration. It is now known that even nocturnal spiders have a good home-finding ability, in both distance and direction. Terrestrial mites feed in various ways, and tactile receptors predominate. It is well known that some spiders and mites live in the pitcher. Therefore, it is difficult—without greater knowledge of the species—to distinguish between animals that have accidentally fallen into the pitcher and animals living normally in pitchers and dying there.

The prey in ground pitchers mentioned above show some common characteristics:

- They are very good runners.
- They are wingless arthropods (except the cockroaches and beetles).
- They are predators (except nectar collecting ants and omnivorous cockroaches).
- They achieve orientation by chemical and tactile receptors (except spiders with few ocelli).
- They exhibit nocturnal activity (except ants).

The conclusion of these facts is that the predators probably fall accidentally into the pitchers. Their populations must be well developed in the *Sphagnum* layers and regenerate quickly. The role of the decaying, smelling organic matter in the pitchers is unclear. Though my investigations are not quantitative, I will discuss some phylogenetic aspects here.

Suppression of pitchers

It is well known that some species of *Nepenthes* possess only ground pitchers (*N. rhombicaulis*, *N. "rosulata"* (This last name is invalid, but is being used to denote plants of *N. gymnamphora*—ed.)) or only short shoot pitchers (*N. ampullaria*, *N. pervillei*). Their long shoot pitchers are suppressed or not developed. This may be caused especially by shade or nitrogen rich soil (see Smythies (1965); Green (1967); Schmid-Hollinger (1979)). But this reduction of hanging pitchers may also be forced through selective pressure by absent prey. In biotopes with few flying insects it seems more economic to give up hanging pitchers. These reflections are not in contradiction to the models of Givnish (1984) (see Juniper *et al.* (1989)). Givnish shows that the cost-benefit analysis of carnivorous plants is rapidly negative in shady places. In shady places the sizes of the *Nepenthes* leaves are often enormous. The photosynthetic parts of the leaves are large and very long. If we follow Givnish, we may explain this excessive growth as due to minerals gained in ground pitchers which enhance leaf growth.

Why such elaborate ground pitchers?

Ground pitchers in mossy forests are successful! As we saw, big insects like cockroaches and centipedes were caught. Ground pitchers show many exciting features: large, intensely coloured peristome, teeth and nectar. But the above cited arthropods do not react to colours, they orient through chemical receptors. A simple funnel without luxurious accessories would have the same effect on these mostly nocturnal arthropods. A possible answer to this conflict may be that the present successful relationship between ground pitchers and ground arthropods is of secondary nature.

In *Nepenthes mirabilis*, Jebb (1989) found similar prey. But he found cockroaches and centipedes also in upper pitchers. It is understood that these arthropods are also good climbers (see also the comment on Jebb by Cheek (1992)).

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Figure 4: Centipede (*Scolopendra*)



Figure 5: Spider as prey

From the pages of CPN 25 years ago

Greenhouse pests plagued a new member (all members were new back then!): “Isamu Kusakabe has noticed that cats are apparently attracted by odor to his *Drosophyllum*. They break into the greenhouse and step all over his other plants in order to get to *Drosophyllums* [sic]. He and we would be interested to know if anyone else has observed this phenomenon.”

And for perhaps the first time in print, we learned how to obtain pollen from *Byblis gigantea*: “Warren Stoutamire noted that the flower has a structure similar to some non-carnivorous plants that require vibration of the anthers by the wings of bees and other insects for dehiscence to occur. Joe Mazrimas tried this and obtained abundant pollen.”

Genetics of *Sarracenia* leaf and flower color

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Abstract

Sarracenia is a genus of insectivorous plants confined to wetlands of eastern U.S. and Canada. Eight species are generally recognized with flower and leaf color ranging from yellow to red. Fertile hybrids occur in the wild under disturbed conditions and can be artificially produced in the greenhouse. Thus genetic barriers between species are weak. Normally when crosses occur or are induced between species or between different color types the progeny exhibit a blending of parental phenotypes called incomplete or partial dominance. In most species all-green mutants have been found which lack any red pigment in leaves, flowers or growth point. Controlled crosses were performed on all-green mutants from *S. purpurea* and two subspecies of the *S. rubra* complex. Self pollinated all-green plants result in all-green offspring and self pollinated wild-type red plants result in red offspring. Crosses between red and all-green plants produce wild-type colored red progeny. These results suggest that the red alleles are "dominant" to the "recessive" all-green mutant alleles in the three independent all-green variants tested. Since partial dominance is the usual genetic pattern in the genus, dominant/recessive characteristics are an unusual phenomenon.

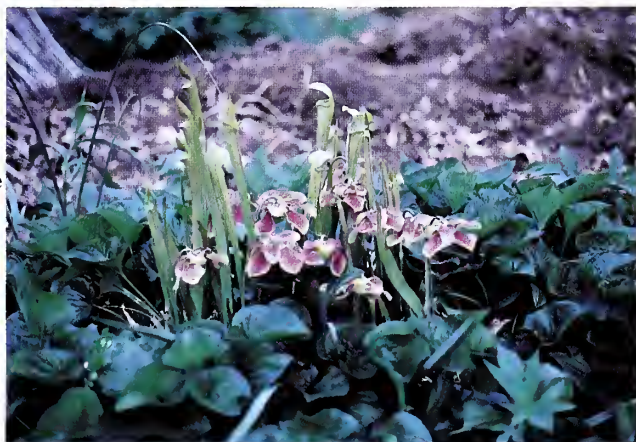


Figure 1: A pink flowered hybrid in cultivation. This specimen was collected by Fred Case and is the cross *S. rubra* subsp. *wherryi* × *S. alata*.

Introduction

The Sarraceniaceae (American pitcher plants) is a family of insectivorous pitcher plants restricted to wet, sunny, generally acid, nutrient poor habitats of

the southeastern United States, Canada, northern California, southern Oregon, Venezuela, British Guiana (Lloyd, 1942), and Brazil (Maguire, 1978). The family contains a total of three genera: *Darlingtonia*, *Heliamphora* and *Sarracenia*. *Darlingtonia* is found in coastal swamps, moist mountain meadows and serpentine creeks of northern California and southern Oregon. *Heliamphora* occurs in savannas and peat bogs of the sandstone table mountains of Venezuela, Brazil, and British Guiana. *Sarracenia* is restricted to acid, moist savannas and seepage bogs of the southeastern United States and acid bogs and alkaline meadows of Canada and the northern U.S.

American pitcher plants are herbaceous, rhizomatous plants which have leaves and stems modified into tubular or funnel shaped structures. These modified leaves catch and digest insects by means of a pitcher or pitfall trap. Presumably insects are attracted by color, scent and nectar to the pitcher mouth although experiments testing this hypothesis need to be done. Insects then lose their footing and fall into a pool of water in the pitcher. Escape is prevented by smooth waxy walls, downward pointing hairs and a stupefying or narcotic agent in the pitcher liquor (Hepburn *et al.*, 1927; Mody *et al.*, 1976). Bacterial and plant enzymes then digest the insect and the by-products are used by the plant for growth (Hepburn *et al.*, 1927; Plummer & Jackson, 1963; Plummer & Kethley, 1964). It is believed that the trapping of insects evolved in order to compensate for the lack of nutrients in pitcher plant habitats (Romeo *et al.*, 1977).

The evolution of the three genera is poorly understood due to the lack of any fossils. Albert *et al.* (1992) suggest an evolutionary relationship among the three genera based on similarities in the plastid *rubisco L* gene.

Botanical treatments (McFarlane, 1908; Uphof, 1936; Bell, 1949; McDaniel, 1966) of the genus *Sarracenia* have led to a general acceptance of eight species: *Sarracenia alata*, *S. flava*, *S. leucophylla*, *S. minor*, *S. oreophila*, *S. psittacina*, *S. purpurea*, and *S. rubra*. *Sarracenia purpurea* has been split into the two subspecies *venosa* and *purpurea*. *Sarracenia purpurea* subsp. *venosa* contains a recently described variety named *burkii* (Schnell, 1993) while *S. purpurea* subsp. *purpurea* has a form lacking purple or red pigment called forma *heterophylla*. Some taxonomists advocate splitting *S. rubra* into as many as three species with two subspecies (Case & Case, 1974, 1976), five species (McDaniel, 1986), one species with five subspecies (Schnell, 1977, 1979b) or just one species (Bell, 1949). The taxonomy of Schnell (1977, 1979b) will be followed in this paper.

Known species flower colors are red, pink, yellow and cream (Table 1). *Sarracenia alata*, *S. flava*, *S. minor* and *S. oreophila* have yellow flowers with *S. alata* variants producing cream flowers. *S. leucophylla*, *S. psittacina*, *S. purpurea* and *S. rubra* have red flowers with variants in all four species producing yellow flowers. *S. purpurea* subsp. *venosa* var. *burkii* has pink to cream flowers. Leaf shapes range from upright to decumbent. Upright species are *S. alata*, *S. flava*, *S. leucophylla*, *S. minor*, *S. oreophila* and *S. rubra*. Decumbent species are *S. psittacina* and *S. purpurea*.

Table 1: Species in the genus *Sarracenia* are normally either red, pink or yellow to cream-yellow flowered. Flowers of normally red flowered species can be yellow, pink flowered species can be cream, and yellow and cream-yellow flowered species can be cream.

<u>Taxon</u>	<u>Normal Flower Color</u>	<u>Variant Flower Color</u>
<i>S. leucophylla</i>	Red	Yellow
<i>S. psittacina</i>	Red	Yellow
<i>S. purpurea</i> subsp. <i>purpurea</i>	Red	Yellow
<i>S. rubra</i> complex	Red	Yellow
<i>S. purpurea</i> subsp. <i>venosa</i> var. <i>burkii</i>	Pink	Cream
<i>S. alata</i>	Yellow/cream	Cream
<i>S. flava</i>	Yellow/cream	Cream
<i>S. minor</i>	Yellow/cream	Cream
<i>S. oreophila</i>	Yellow/cream	Cream

Wild-type *Sarracenia* plants contain some purple or red pigment in either the growth point, leaves, flowers or a combination of the three. Normally, species leaf color can be either red, yellow, purple, red striped and splotched. Striped or splotched individuals possess a yellow background with varying intensities of pigmentation. Yellow leaved individuals maintain pigment in the growth point which is brilliant reddish-purple. Leaf and flower color variation have been extensively discussed in the literature (Masters, 1881; McFarlane, 1908; Bell, 1949; Case, 1956; McDaniel, 1966; Schnell, 1978b, 1979a, 1993).

Flower color, leaf color, leaf shape and leaf number are both genetically and environmentally controlled (Bell, 1949; Mandossian, 1966a; Schnell, 1978b). As an example I have observed that red-flowered species growing in shaded habitats will produce flowers that are still red but not as *intense* as those growing in full sun. Yellow-flowered species maintain yellow in the shade but the color may not be as vibrant. Low light levels may result in reduction of pitchers to flattened leaves. Soil pH can effect the number and size of leaves but has no effect on color. The effect of environment is most pronounced in pigment production in the leaves. Individuals with a genetic predisposition to be red show these characteristics best in full sun. Root disturbance or shading can result in reduction in quantity and distribution of red pigment.

Offspring of crosses between *Sarracenia* species or varieties normally exhibit blending of the parental characteristics (Russell, 1919) called incomplete or partial dominance. As an example, crosses between red- and cream-flowered species typically produce hybrids with pink flowers (Figure 1). Species can be easily crossed and the resulting hybrids can be back-crossed with the parents without deleterious effect on offspring fertility. Natural hybrids are known between almost all species in the genus (Bell, 1952; Bell & Case, 1956). Hecht (1949) reported a reduced chromosome number of n=12 for all species in the genus while Bell (1949) identified one more chromosome and arrived at n=13 which is now the accepted figure.

The species distinction in plants allows for hybrids to occasionally occur between taxonomically recognized species (Jones & Luchsinger, 1986). In *Sarracenia* barriers between species interbreeding are not dictated by a difference in chromosome numbers. Rather, species integrity is maintained by a combination of different flowering times, flower color and habitat preferences (Bell, 1949).

Two recurring unusual variant forms are found, however, in the genus *Sarracenia*. The first involves the total lack of red or purple pigment in leaves, flowers and growth point (hereafter called "green") and the second is normally red-flowered species that are yellow-flowered. The green variant of *S. purpurea* subsp. *purpurea* was recognized as early as 1822 by Eaton (Eaton, 1822, 1833) and is known as f. *heterophylla*. Both variants have been found in a number of species at a variety of locations over the past fifty years (Robinson, 1981; Sheridan & Scholl, 1993a, 1993b; Shomin, 1993). Green or yellow-flowered variants occur singly or as a few individuals intermixed with normal wild-type plants in the field (Case, 1956; Sheridan & Scholl, 1993a, 1993b).

Scholl (1994) and Baumgartl (1993) report individuals of *Heliamphora* which lack purple or red pigment in the leaves and are analogous to the green variant. Unfortunately research can not be pursued in this genus at this time due to insufficient plant material and breeding problems. Yellow-flowered variants in *Sarracenia* are also limited in number and require several years to reach maturity and for these reasons this study focused specifically on the genetics of red and green leaf color in *Sarracenia*.

In preliminary, casual work with *Sarracenia*, Bill Scholl and I (1993b) observed that when red or green plants were self-pollinated the offspring were true-breeding red or green. When red and green plants were reciprocally crossed the offspring from each parent appeared to be a mix of red and green plants. The purpose of this study was to perform controlled matings between green plants of *S. purpurea*, *S. rubra* subsp. *gulfensis* and *S. rubra* subsp. *jonesii* and red plants of the same or similar subspecies in order to determine the validity of our casual observations and to begin elucidation of the genetic interactions between wild-type red and green alleles.

Materials and Methods

Plants of *Sarracenia* were brought from winter storage in Caroline County, Virginia and placed in the Virginia Commonwealth University (VCU) greenhouse from 17 March—24 March (1993). Plants in need of repotting or those collected bare root from a research bog were planted in a 50/50 mixture of Canadian peat moss and sandy soil collected on the Reedy Creek drainage in Caroline County. Potted plants were then assigned a clone number and placed in a 2 mil (0.05 mm) thick plastic lined bed measuring 90 × 240 cm (3 × 8 ft) with a southern exposure in the VCU greenhouse in Richmond, Virginia. The bed was then filled to a depth of 5 cm (2 in) with deionized water. Water level was maintained at this level on a daily basis.

Additional plant specimens remained in the research bog and were allowed to grow under natural conditions and flowering times. Their treatment of flower covering and pollination was the same as plants maintained in the greenhouse as discussed below.

As flowers emerged they were covered securely with tobacco netting before flower maturity and pollen deposition to prevent possible insect pollination. In most cases there were extra flowers on a clone involved in a cross which served as controls. Most of these flowers were covered in a similar manner but a few were left uncovered to see if any pollinator activity might occur in the greenhouse.

As soon as pollen was observed in the flower, self and cross pollinations were performed. Pollinations were done by first removing netting from the flower and then dipping a clean toothpick in vegetable oil. Pollen was scraped from the umbrella with the oiled toothpick and placed on all stigma tips of the pollinated flower. After each pollination the toothpick was discarded and a clean toothpick obtained for additional crosses. Toothpicks were only dipped once in vegetable oil and at no time were redipped after contacting pollen. After a cross was done a plastic label with an alphanumeric identifier was attached to the flower designating the cross.

After petals dropped, netting was removed from flowers. Plants were then returned to irrigated beds in Caroline County and ovaries were allowed to mature over the summer. Seed-containing capsules were harvested from 11 August–18 August (1993) and allowed to air dry in labeled film vials at room temperature for two weeks. Following drying, vials were closed and placed in a refrigerator maintained at 4°C at VCU.

The number of seeds per capsule was then determined by first separating and discarding capsular debris. Seeds were counted and then returned to the refrigerator in film vials.

After all seeds had been counted and cleaned, ten seeds each were placed in ten labeled 5.5 coin sub. 24 Universal Brown Kraft envelopes for a total of one hundred seeds for each capsule. Seeds from capsules of the same type of cross were not mixed. In this manner every capsule from a cross was allotted a test of one hundred seeds. In cases where a capsule produced less than one hundred seeds all seeds were sown. Two inch square plastic pots were filled to within 1.3 cm (0.5 in) of the top with a premoistened 50/50 sand and peat mixture and placed in plastic lined trays measuring 46 × 2 × 85 cm (18 × 11 × 2 in). Seeds were then sown in pots by tapping the contents of a single labeled envelope into a single pot and placing identifying labels in each pot. Trays were placed in a 4°C refrigerator and the seeds were allowed to stratify (a period of cool, moist conditions is required for germination). Two repetitions were done in this manner. The first was in stratification from 27 November 1993–24 January 1994 and the second from 28 December 1993–4 February 1994 for a total stratification period of 59 and 39 days respectively.

At the end of the stratification period seed trays were brought into the greenhouse and placed under continuous illumination by 1.3 m (4 ft) cool white fluorescent lamps. Trays were placed on a metal stand with four trays per bank of five fluorescent lights. The total assembly contained four vertical sets of trays with fluorescent lights placed 13 cm (5 in) from the soil surface.

Pots were kept at constant moisture levels by maintaining 2.5 cm (1 in) of deionized water in the trays. High and low air temperature in the growth area was monitored on a daily basis with a minimum/maximum thermometer.

Initial germination of seedlings was noted and development observed. On 22 March 1994 the numbers of red and green seedlings per pot were noted and the percent germinations determined by dividing the numbers of seedlings by total numbers of seeds sown.

The above procedure was followed for the third replicate and for selected repeated crosses performed in 1994 with the following exceptions.

1. Netting over flowers was not removed from 1994 crosses until harvest time in mid-August.

2. All seeds of a cross were dusted with the fungicide Captan and were sown at the same time in fiberglass "Permanest" trays measuring 22 × 30 cm (8.5 × 12 in). Soil moisture was maintained by removing a row of soil on the edge of the tray and irrigating via this "drainage ditch".

3. 1994 crosses were harvested on 13 August 1994, stratified starting 8 November 1994 (2 November 1994 for replicate 3) and placed under lights 23 December 1994. Assessment of seedling phenotype and repotting of seedlings was done from 26 June—2 July 1995.

Results

10,202 seeds were produced as a result of twenty-two crosses with germination averaging 23% between the three replicates in 1993 crosses (Table 2a). 4042 seeds were produced in four crosses in the 1994 repetition of selected crosses with germination averaging 35% (Table 2b). One viable seed was produced by a control flower in 1994 (#156) while no seeds were produced by other controls. No germination occurred with crosses involving plants #71 and #116. Seed was produced by plant #32B and #35A even though they were not intentionally pollinated.

Reds in two species were self-pollinated once with one repetition and greens in one species and two subspecies were self-pollinated six times with possibly two additional unintentional self-pollinations and one repetition. Greens were pollinated by reds six times and reds pollinated with greens four times (one repetition of each). Self-pollinations of green plants resulted in green seedlings with one exception in 1994 (cross #114A) where one red seedling was produced. Self-pollinations of red plants resulted in red seedlings with one exception in the third replicate in 1993 where three greens were produced (cross #113A). Reciprocal

crosses of red and green plants resulted in red seedlings (Table 3). Greenhouse temperatures averaged 30°C with highs reaching 51°C and lows to 15°C.

Discussion

Overall germination rate and the difference in percent germination between replicates and the repetition may have several explanations. Mandossian (1966b) found optimal germination of *S. purpurea* occurred at 28°C but inhibition and/or death of seed/seedling occurred at 33°C. Replicate 1 seeds were placed on the low-tier tiers of the light racks while replicate 2 was on the top tiers. It is possible that heat from the fluorescent light ballasts along with warm days in the greenhouse may have elevated temperatures in the upper tiers to lethal levels. Greenhouse highs of 51°C were recorded and this would have been lethal if sustained. These high temperatures, however, were not sustained or the normal environment. Other factors to consider are stratification and water mold. Mandossian (1966b) got germination rates averaging 59% in constant light at 28°C between one, two and three month prechills. Thus stratification time in this experiment was probably not a factor in germination rate. Rather the most likely culprit was an outbreak of water mold on the seeds as they were in stratification. I have since gone to one month prechills with dusting the seeds in Captan and this seems to control the deleterious effects of water mold on seeds. In addition, initial drying of seeds in Caroline County in film vials resulted in fungus attacks on the drying seeds.

The lack of germination in #71 and #116 was likely due to two reasons. Plant #71 was attacked by a fungal infection soon after pollination and most of the plant was destroyed in the attack and the flower stalk withered. Seeds were not fully developed. Plant #116 was in the research bog and the seedpod was attacked at maturity by a seed eating larva. Apparently seeds that appeared undamaged may have been incapacitated by the larva in some manner.

It is interesting to contrast my preliminary work (Sheridan & Scholl, 1993b) in which reciprocal crosses produced both red and green offspring and the results of this study where only one phenotype (red) was produced by this cross. This difference may be explained by the manner in which the preliminary work was done. Although flowers were covered to prevent accidental pollination, the assistant employed in performing the pollinations may have contaminated the crosses by tainting the oil with pollen or any one of the previously mentioned scenarios could have occurred. In any case the carefully controlled crosses of this experiment did not fully support my earlier observations of mixed red and green progeny in reciprocal crosses with this genus.

Various growers have postulated that green forms in *S. purpurea* arise by a gradual progression from red forms to lighter colored intermediates to the green form indicating polygenic inheritance or codominance. In polygenic inheritance an additive effect is seen on the phenotype through the cumulative effect of a number of genes (Klug & Cummings, 1991). In *S. flava* leaf color variants range from red to yellow with various intermediate color variants. This range of color in *S. flava* could indicate an additive effect of color genes in this species. Unfortunately no formal experiments have been conducted in any *Sarracenia* species to actually

test whether partial dominance or polygenic inheritance is actually occurring although it is indicated by field observations.

The results of this experiment, however, do not support polygenic inheritance or partial dominance (blending) between green and red *Sarracenia* varieties. Rather a dominant/recessive genetic basis is indicated. Red is dominant to a recessive green since only red was seen in reciprocal crosses and red self-pollinations, not an intermediate color. Green was only seen in self pollination of green plants (exceptions are discussed below). When only one of two parental phenotypes is observed in crosses, the trait is said to be dominant to the washed or hidden trait, which is said to be recessive. Since all reciprocal crosses of red and greens were red, I conclude that the red allele is dominant to the green allele. Thus dominant/recessive characteristics represent an unusual genetic behavior in the genus *Sarracenia*.

Different crosses have been made by *Sarracenia* growers between greens in different species and in every case the result has been green offspring. One interpretation of these results is that the occurrence of greens in different species is caused by mutations effecting the same gene. If crosses between greens in different species had resulted in reds then different genetic events might be suspected to account for the occurrence of green plants in different species. Since greens are produced, mutation of the same gene is probably sporadically occurring throughout the genus.

The production of viable seeds by plants #32B, #35A and #156 may support Mandossian's assertion (1965) that a certain amount of self-pollination may occur in *Sarracenia*. It is also possible that the retrieval of pollen from flowers #32B and #35A for other crosses may have inadvertently resulted in some self pollination even though the stigmas were not touched. Plant #156 was in the research bog in Caroline County and was not handled at all after covering. I suggest that the limited amount of self pollination observed by Mandossian and myself is due to a small amount of airborne pollen landing on stigma tips.

The occurrence of a few green seedlings in the selfing of a red (third replicate in cross #113A) and a red seedling in a selfed green (cross #114A in 1994 repetition) may have several explanations. These two plants were growing intertwined at the same research bog in Caroline County, Virginia as control #156. There are several possible explanations for these outcomes.

1. Pollen was blown from one plant and landed on the stigma tips of another managing to circumvent the netting in both cases. This would explain the occurrence of a red in a green but not a green in a red self-pollination under a dominant red/recessive green situation.

2. Green reverted (mutated) back to red and a red mutated to a green.

3. Seeds jumped inadvertently during watering or other handling. *Sarracenia* seeds are very hydrophobic and extreme care must be exercised in the watering process to avoid seeds jumping during contact with falling water droplets and sub-

sequent contamination of other pots.

4. Although I like to say my bags are insect-proof I have observed that small ants are able to penetrate small gaps at the tied stalks in bagged flowers and harvest nectar from the base of the ovaries in outside pollinations. Although these are by no means the main pollinator it is possible that they could transfer a small amount of pollen to a stigma tip in their foragings.

5. A combination of all of the above could occur.

To reduce or eliminate the possibility of accidental selfing, crossing or seed contamination during stratification or germination I would make the following suggestions to other workers.

1. An effective and efficient system of flower emasculation needs to be developed to perform large scale crosses. Mandossian (1965) commented on how time consuming and damaging to the flowers this process can be. I experimented with this process on a flower prior to petal descent but pollen grains were still being dislodged and I considered the process potentially more contaminating than a careful cross.

2. Perform crosses between physically different species. This would tend to eliminate an obvious self pollination but we should keep in mind that the genetics of this group is being sorted out and a cross potentially may look like one of the parents.

3. Immediately after sowing trays should be covered with a transparent protective covering. I am now using glass plates or plastic domes to cover a particular tray. Covers should remain on through stratification and initial germination until repotting of seedlings. Obviously, the time of year has to be considered in this to avoid cooking the seedlings and lids can be vented to reduce heat buildup.

This experiment demonstrated that the green trait can be transmitted through the seeds in self pollination of green plants but does not answer how it arises in the wild. Conservation work at the Atlanta Botanical Garden by Ron Determan has helped to shed some light on how green forms are occurring in the wild. Two green seedlings of *S. rubra* were isolated out of four capsules collected along a creek in western Georgia. The remainder of the seedlings were all wild-type. All seed came from a local, vigorous colony of wild type plants where only *S. rubra* now grows.

In addition, Bob Hanrahan (1994) reports that he has isolated green seedlings of *S. purpurea* subsp. *venosa* from wild seed on several different occasions.

At least two scenarios could explain how Mssrs. Determan and Hanrahan obtained green plants from populations of wild-type reds. Either a premitotic mutation occurred or there was a preexisting mutation present in the population. A premitotic mutation from red to green could result in a flower bud with varying degrees of heterozygosity in the ovules. The seed yield of a plant of *S. rubra* used

in this experiment (#23B) from the same region of Georgia that Ron Determan obtained his seed was 154 seeds. Since this experiment yielded a 23% germination rate, a capsule of 154 seeds would germinate 35 seeds ($154 \text{ seeds} \times 23\% = 35 \text{ seeds}$). The proportion of recessive greens expected from self pollinating a heterozygous individual would then be nine seeds ($35 \text{ seeds} \times 25\% = 9 \text{ seeds}$). Given that some outcrossing will probably take place in the field a yield of two green seedlings from a heterozygous plant is within the realm of possibility. If the plant was only 1/4 heterozygous due to a premitotic mutation two green seedlings is entirely realistic.

The second possibility is that a preexisting green individual was in the area at one time or that heterozygotes are present. Sheridan & Scholl (1993b) and Troup & McDaniel (1980) have extensively explored the area prior to Determan's work and no green plants were observed. Also, pitcher plant pollen is carried locally (within one mile) by *Bombus* species (Schnell, 1983) which would preclude long distance pollination by a distant green form. It is unlikely then that a green plant is in the immediate area. However, the chance that a heterozygous individual is present is much more likely. When Mr. Determan harvested seed he may have retrieved only one or the only capsule from a heterozygous plant. Using the same arithmetic as above, two green seedlings could be obtained from a heterozygous individual. Green may have a low frequency in the population and thus is rarely seen.

Schnell (1978a) concluded leaf color variation in *S. flava* was non-adaptive while Bell (1949) suggested that the reproductive success of the green *S. purpurea* subsp. *purpurea* f. *heterophylla* might have some selective advantage. If green is occurring at a low frequency what are the selection pressures (if any) for or against the allele? Further genetic experiments as well as studies of prey capture effectiveness of red and green variants are warranted. Studies of pollination and resultant seed set of red and green variants in natural conditions are being studied at this time.

It is worth commenting on the direction of change in yellow flower color variants even though these plants were not examined in this study. Flower color changes from red to yellow but not the reverse. No variants in a yellow-flowered species have been found which spontaneously become red-flowered. Schnell (1978b) found that red-flowered species have red pigment on a yellow background. This could indicate that the development of yellow-flowered individuals from red-flowered species could be due to the loss or suppression of a gene controlling red pigment production in flowers. The all-green mutant forms studied in this experiment may be experiencing mutation of the same gene yet earlier in the metabolic pathway which controls leaf, flower and growth point color.

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Table 2a:
Seed Produced and Percent Germination in 1993 Crosses

<u>Cross #</u>	<u>Seed Yield</u>	<u>Rep. 1</u>	<u>Rep. 2</u>	<u>Rep. 3</u>	<u>Type of Cross</u>
10	116	28/100	2/17	—	green selfed
22A	164	49/100	18/64	—	red × green
23A	378	54/100	23/100	42/88	red × green
23B	155	46/100	16/55	—	red selfed
29A	269	38/100	9/100	0/9	green selfed
30.1	288	34/100	10/100	—	green selfed
30.2	78	23/100	—	—	green selfed
32A	597	37/100	19/100	79/307	green × red
32B	76	35/100	—	—	green selfed?
35A	63	20/100	—	—	green selfed?
37.1	354	37/100	38/100	31/64	green × red
37.2	462	43/100	20/100	38/172	green × red
71A	390	0/100	0/100	0/100	red × green
71B	409	0/100	0/100	0/119	red × green
113A	1540	14/100	5/100	224/1250	red selfed
113B	1641	21/100	6/100	165/1351	red × green
114A	945	31/100	14/100	212/655	green selfed
114B	1586	25/100	9/100	573/1296	green × red
115B	335	54/100	39/100	3/45	red × green
116A	86	0/100	—	—	green selfed
116B	22	0/100	—	—	green × red
117	<u>248</u>	<u>37/100</u>	<u>14/100</u>	<u>—</u>	green × red
Total	10,202	626/2200	242/1536	1367/5456	
Average	464	29%	16%	25%	

Table 2b:
Selected Repetitions of 1993 Crosses Performed in 1994
(Seed Produced and Percent Germination)

<u>Cross #</u>	<u>Seed Yield</u>	<u>Germination</u>	<u>Type of Cross</u>
113A	1373	102/1373	red selfed
113D	927	280/927	red × green
114A	860	609/860	green selfed
114B	881	404/881	green × red
156	<u>1</u>	<u>—</u>	control
Total	4042	1395/4041	
Average	1010	35%	

Table 3
Outcome of Self and Cross Pollinations

3A. *S. rubra* subsp. *gulfensis* (green)

<u>Cross #</u>	<u>Type of Cross</u>	<u>Seedling Phenotype</u>
10	green selfed	green
117	green × red	red

3B. *S. rubra* subsp. *jonesii* (green)

<u>Cross #</u>	<u>Type of Cross</u>	<u>Seedling Phenotype</u>
22A	red × green	red
23A	red × green	red
23B	red selfed	red
29A	green selfed	green
30.1	green selfed	green
30.2	green selfed	green
32A	green × red	red
32B	green selfed?	green
35A	green selfed?	green
37.1	green × red	red
37.2	green × red	red
115B	red × green	red
116A	green selfed	green
116B	green × red	red

3C. *S. purpurea* subsp. *purpurea* f. *heterophylla* (green)

<u>Cross #</u>	<u>Type of Cross</u>	<u>Seedling Phenotype</u>
113A	red selfed	red (3rd rep 1993 had three green seedlings)
113B	red × green	red
114A	green selfed	green (1994 one red seedling)
114B	green × red	red
156	control	green

Appendix: Identity of crosses

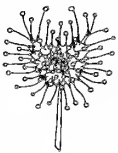
<u>Cross #</u>	<u>Identity</u>
10	<i>S. rubra</i> subsp. <i>gulfensis</i> (green)—selfed
22A	<i>S. rubra</i> (red-Taylor Co., Ga.) × <i>S. rubra</i> subsp. <i>jonesii</i> (green)
23A	<i>S. rubra</i> (red-Taylor Co., Ga.) × <i>S. rubra</i> subsp. <i>jonesii</i> (green)
23B	<i>S. rubra</i> (red-Taylor Co., Ga.)—selfed
29A	<i>S. rubra</i> subsp. <i>jonesii</i> (green)—selfed
30.1	<i>S. rubra</i> subsp. <i>jonesii</i> (green)—selfed
30.2	<i>S. rubra</i> subsp. <i>jonesii</i> (green)—selfed
32A	<i>S. rubra</i> subsp. <i>jonesii</i> (green) × <i>S. rubra</i> (red-Taylor Co., Ga.)
32B	<i>S. rubra</i> subsp. <i>jonesii</i> (green)—selfed
35A	<i>S. rubra</i> subsp. <i>jonesii</i> (green)—selfed
37.1	<i>S. rubra</i> subsp. <i>jonesii</i> (green) × <i>S. rubra</i> subsp. <i>jonesii</i> (red-Etowah, N.C.)
37.2	<i>S. rubra</i> subsp. <i>jonesii</i> (green) × <i>S. rubra</i> subsp. <i>jonesii</i> (red-Etowah, N.C.)
71A	<i>S. rubra</i> subsp. <i>jonesii</i> (red-Etowah, N.C.) × <i>S. rubra</i> subsp. <i>jonesii</i> (green)
71B	<i>S. rubra</i> subsp. <i>jonesii</i> (red-Etowah, N.C.)—selfed
113A	<i>S. purpurea</i> (red-Reynolds Pond, Del.)—selfed
113B	<i>S. purpurea</i> (red-Reynolds Pond, Del.) × <i>S. purpurea</i> forma <i>heterophylla</i> (green)
113D	<i>S. purpurea</i> (red-Reynolds Pond, Del.) × <i>S. purpurea</i> forma <i>heterophylla</i> (green)
114A	<i>S. purpurea</i> forma <i>heterophylla</i> (green)—selfed
114B	<i>S. purpurea</i> forma <i>heterophylla</i> (green) × <i>S. purpurea</i> (red-Reynolds Pond, Del.)
115B	<i>S. rubra</i> subsp. <i>jonesii</i> (red-Greenville Co., S.C.) × <i>S. rubra</i> subsp. <i>jonesii</i> (green)
116A	<i>S. rubra</i> subsp. <i>jonesii</i> (green)—selfed
116B	<i>S. rubra</i> subsp. <i>jonesii</i> (green) × <i>S. rubra</i> subsp. <i>jonesii</i> (red-Greenville Co., S.C.)
117	<i>S. rubra</i> subsp. <i>gulfensis</i> (green) × <i>S. rubra</i> subsp. <i>gulfensis</i> (red-Blue Ridge Rd.)
156	<i>S. purpurea</i> forma <i>heterophylla</i> (green)—control

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The Savage Garden

PETER D'AMATO
Fertilizing Carnivores

Keywords: cultivation: fertilizers

There are two basic rules of green thumb concerning the application of artificial fertilizers on carnivorous plants: strongly dilute the fertilizer, and apply it as a foliar feed. That most plants can absorb minerals through their leaves is well known in horticulture. Spraying the foliage of plants with a fertilizer can be as effective as feeding them through their roots. This is also true with carnivorous plants; since most of their leaves are specially adapted to absorb minerals through

specialized digestive glands, artificial fertilizers can be as readily absorbed as insect prey. By applying fertilizers to the leaves and not the soil, you will not have to worry about hanging the mineral content of the plant's nutrient poor medium.

First, some general guidelines. If your plants are receiving a steady diet of insects, it is probably not necessary to feed them. But you may want to supplement their diets to try to grow even more vigorous plants. Or you might be growing carnivorous plants in a terrarium and may not want to hassle with feeding them insects. Perhaps you wish to display a plant at an upcoming flower show, and would prefer to present a beautiful but clean specimen, without the carcasses of digested insects distracting from the beauty of the leaves.

Some varieties of carnivorous plants benefit from a regular fertilization program. Others, however, seem to detest it. There are many fertilizers on the market developed for a wide variety of plants and purposes, and different products are available in different countries, but nowhere has a commercial fertilizer ever been developed specifically for carnivorous plants. Therefore, we must select and experiment from the general forms of fertilizers available.

Fertilizers For Acid-Loving Plants

These are readily available in most general nurseries. They are used for plants that prefer an acid soil, such as pines, firs, rhododendrons, and so on. Since many carnivorous plants grow in acid soils, this form of fertilizer is useful. I have used it successfully on all *Sarracenia* species, *Darlingtonia*, most but not all *Drosera*, temperate, acid-loving *Pinguicula*, most *Utricularia*, and *Dionaea*. Avoid using it on tropical *Pinguicula* and most *Nepenthes*.

Orchid 30-10-10

This form of plant food is used to promote foliage growth, as opposed to those formulated to stimulate flowering. I have used various brands on *Nepenthes*, *Heliamphoras*, tropical *Pinguicula*, most terrestrial *Utricularia*, and I believe it can be used successfully on most of the plants enjoying acid conditions as well.

Epiphyte Fertilizers

You may have to hunt for these in your nursery, as they are specifically developed for epiphytes such as *Tillandsia* and other Bromeliads. These plants live in tree branches high above the ground, where they obtain nutrients from small amounts of leaf debris that collect on their leaves and roots. Like carnivores, they absorb much of their nutrients through their leaves. Epiphyte fertilizers were developed to enhance mineral absorption through the leaves, and therefore can be quite beneficial to carnivorous plants. I have used brands such as "Epiphytes Delight" on all carnivorous species except those few which seem to dislike any fertilization.

Fertilizers for carnivorous plants are usually best when diluted to 1/4 or 1/2 of the manufacturer's directions. It can then be sprayed on the leaves of the plant. Thoroughly wet the foliage. It is usually necessary to do this only once or twice monthly during the growing season. Do not fertilize dormant plants! You can also

apply fertilizer to the soil of some plants that are grown with good drainage and are watered frequently from overhead with purified water. Plants-grown this way, such as *Nepenthes* in a greenhouse, will have excess minerals leached out of the soil every time the plants are watered. Therefore the much feared mineral build-up is avoided.

I would not otherwise apply fertilizers to the soil, especially in undrained containers such as bog gardens. Over time the excess minerals will accumulate in the medium and possibly harm the plants. Some growers prefer to fertilize their plants more frequently using a more heavily diluted ratio. For instance, a 10% solution applied weekly *Sarracenia* can work well. Three plants that are damaged by fertilizers are all sundews: *D. schizandra*, *prolifera* and *adela*.

Be warned that if you mist or spray fertilizers onto carnivorous plants, some will fall upon the soil surface and encourage algal growth. Algae will also grow in water trays and it is wise to clean these periodically. Algal growth on soil can be scraped away with a spoon when the build-up becomes substantial. Replace it with fresh soil. Club-mosses (*Lycopodium*) and other mosses will often utilize the small amounts of fertilizers that fall upon them from mists or sprays. However, *Sphagnum* dislikes fertilizer build-up and usually only succeeds in pots that are frequently leached with pure water.

It is not wise or necessary to apply fertilizers directly into pitcher leaves. This can upset the delicate chemical balance of their digestive juices, and will often encourage the growth of algae. Simply misting the foliage will benefit the plant enough.

Vitamin B1 is a supplement for plants commonly available in nurseries, and most popular is the american brand "Superthrive." This includes other vitamins and ingredients in its solution. These are not fertilizers as commonly supposed, and their use is often controversial among carnivorous plant enthusiasts. Some growers greatly applaud their use, while others find their benefits dubious. I have found products such as Superthrive good for carnivorous plants when one follows the manufacturer's instructions. Vitamin B1 has long been used as an ingredient for promoting root growth, primarily for garden and house plants. It is most often used when transplanting bare-rooted plants, and helps them overcome shock by encouraging root growth. Bare-rooted plants are usually soaked in a solution of 10-25 drops per gallon of water for half an hour or so before they are put into soil. For general plant care, manufacturers of products such as Supertrive recommend a "one-drop-per-gallon" application with each regular watering. I have noticed that bare-root soaking of carnivorous plants in Superthrive or vitamin B1 during the process of transplanting them can reduce losses due to shock. It is particularly helpful when deflasking tissue-cultured carnivorous plants. Using it has reduced considerably my plant losses due to shock if all other conditions were good. Keep in mind that a general application of such products in high doses will increase the growth of algae even more dramatically than fertilizers. So do not apply large doses directly to the soil.

ICPS SEEDBANK

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Updated April 23, 1997

Darlingtonia californica	D. binata North Plains, NZ
Darlingtonia californica Florence OR	D. brevifolia white flower Hampstead, NC
Dionaea muscipula	D. burmannii
Drosophyllum	D. burmannii 'Beerwah, Qld'
Nepenthes rafflesiana	D. capensis
Nepenthes rafflesiana "shadeborne"	D. capensis "green"
Nepenthes (mirabilis X amp) x rafflesiana	D. capensis "wide"
Nepenthes fuskana x rafflesiana	D. capensis "narrow leaf"
Pinguicula ionantha Ltd	D. capensis "white flower" or alba
Pinguicula caerulea due 4/20	D. capensis "purple flower"
Utricularia dichotoma 'Esperance'	D. capillaris
U. gibba	D. dielsiana
U. subulata	D. filiformis filiformis
U. subulata large flower	D. intermedia
Sarracenia flava	D. intermedia v. US
S. flava Ben Hill Cty, Georgia	D. marchantii marchantii
S. leucophylla Swamp in Florida	D. montana
S. minor Fitzgerald, Georgia	D. nidiformis
S. psittacina	D. rotundifolia Rochester NY Ltd
S. purpurea purpurea	D. sessifolia
S. purpurea purpurea NC Mountains	D. spatulata
S. X alata x leucophylla	D. spatulata Hairy Sepals, Gympy Qld
S. X flava X leucophylla "Milton"	D. spatulata pink flower
S. X leucophylla x (flava x leucophylla) Ltd	D. spatulata Kanto
S. X (oreophila x purpurea purpurea) x self	D. spatulata v. Kansai from Japan
S. X purpurea x alata Ltd	D. spatulata Mt. Bartlefreare, QLD
S. X (purpurea x oreophila) x self	D. species Magaliesburg
Drosera aliciae	D. X dielsiana x Sp. Transvaal
D. auriculata Ltd	
D. binata dichotoma small	

All seed contributions are gratefully accepted. Please forward to the above PO Box. Please protect the seeds from postal abuse. I use bubble wrap, although it does require an additional eleven cents in postage (within US). Note: Ltd. means the seeds are in very limited supply.

Please mail comments to: tjohns@primenet.com
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